CHAPTER 20

SPECIATION IN HAWAIIAN CRICKETS

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Hawaii has at least twice as many cricket species[1] as the continental United States; in numbers per unit area it is 1200 to 2500 times as rich. What modes of origin are indicated by such an outburst of speciation? As with other Hawaiian plants and animals, this diversity can be explained only by some favorable balance between rates of speciation and extinction. This chapter attempts through the study of crickets to address several unanswered questions about speciation in Hawaii. Where possible, I make comparison with *Drosophila*. The arguments are drawn from data appearing in detail in a forthcoming book on the biogeography and systematics of Hawaiian crickets (Otte and Rice 1989).

Since the archipelago is isolated by expanses of water great enough to impose barriers to all but a minute number of lucky dispersalists, its biota has evolved more or less independently of those elsewhere on the globe. Interisland isolation is also great and allows for a degree of independent evolution of communities on each island; therefore, within the archipelago a set of natural experiments can test the effects of age, topography, island size, and other factors on speciation rate and the structure of communities. Because of the rarity of immigrants, local (within-island or within-volcano) communities could evolve their own unique characteristics without being disturbed by a continual inflow of migrants.

In this chapter I focus on questions that since Darwin have remained at the forefront of discussions on the origins of species: When do the signal differences (premating barriers) arise in relation to geographic and ecological isolation? What are the principal creative forces that produce the differences? What kinds of extrinsic barriers or partial barriers to interbreeding lead to speciation? Finally I will address the question of why there are so many Hawaiian cricket species and whether Hawaiian speciation is unique in other than trivial ways. I believe Littlejohn (1988) is quite correct in his assessment that "most of the speciational situations with which we deal will already be stabilized, optimized states, with the appropriate evolutionary adjustments having already occurred, so that only the successful systems are available for study. Indeed, it may require a great deal of good fortune to encounter dynamic evolution of a biocommunicative system in natural populations."

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[1] I use Wright's (1978) population concept of species: "The term species has now come to refer to arrays of populations where there is sufficient continuity of interbreeding to give intergradations of all characteristics among local populations, but absence of such intergradation with populations that are considered to constitute other species. [The] occurrence in the same region of two distinguishable populations which do not interbreed is ordinarily taken to indicate that these belong to different species. [And because speciation is often still in progress] all sorts of mixtures and gradations are to be expected."

BACKGROUND

Origins. The Hawaiian endemic crickets appear to be derived from four original colonizing species and from two probable sources: a tree cricket (Oecanthinae) and a sword-tail cricket (Trigonidiinae) from the Americas, and two ground crickets (Nemobiinae) from the western Pacific region (Figure 1). Three of the four original species radiated extensively, although patterns of multiplication along the archipelago have varied according to where each group originated and how it dispersed. Much later, and probably aided by man, eight additional crickets colonized the islands, six from Asia (via the western Pacific), one from Africa, and one from either Africa or Southeast Asia (Otte and Rice 1989). These introduced species are widely distributed along the island chain.

All original colonists probably belonged to flightless species that arrived in Hawaii as eggs deposited in floating vegetation[2]; two of them (tree crickets and sword-tail crickets) were probably forest-inhabiting species and two others inhabited shorelines (coral or rocky shores, or mangrove swamps). Tree and sword-tail crickets may have gained a foothold in lowland forests; from there they expanded into all wet lowland forests and finally into montane forests. Being flightless, the lateral movement of the early colonists within islands must have been relatively slow (in contrast to the more rapid expansion of recently introduced flying crickets), being impeded on younger volcanoes by lava fields, and on older islands by inhospitable ridges and cliffs. Dispersal may have been easiest at a time when there were few competing species to act as obstacles.

[2] The recent (October 1988) flight of a swarm of African desert locusts (*Schistocerca gregaria*) across the Atlantic in a tropical storm originating off the African coast holds open the possibility that crickets could similarly have been transported from the American coasts to Hawaii on storms, which occasionally follow that path.

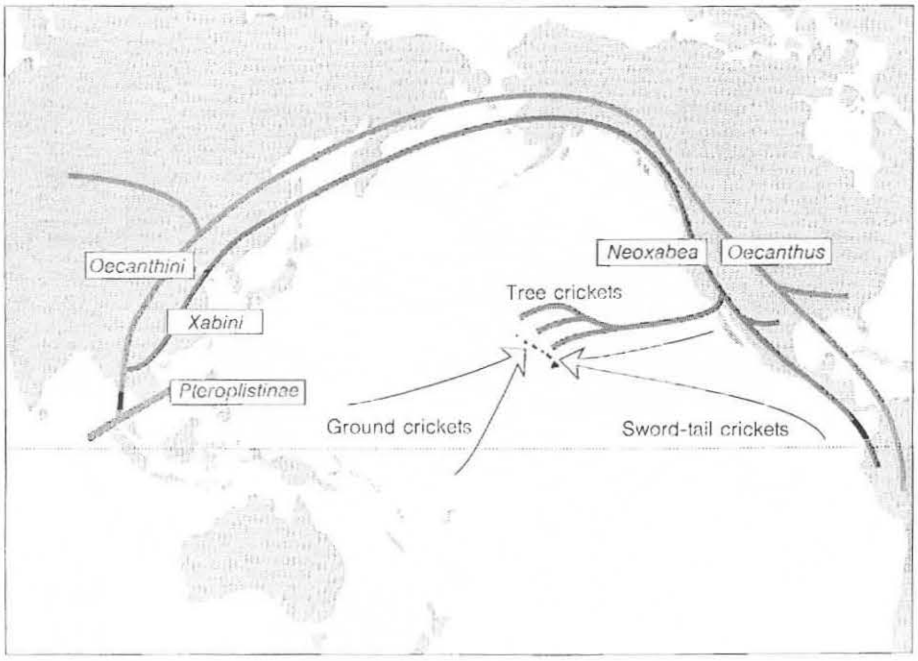

FIGURE 1. Probable origins of the endemic Hawaiian crickets. (From Otte and Rice 1989.)

Aside from the ground crickets, which are rock-adapted and live in coastal or interior lava, virtually the entire fauna is adapted to forests below 4000 feet elevation. This inability to colonize higher forests or to penetrate dry forests on leeward slopes remains puzzling, given the overall success of crickets on the islands. Did becoming adapted to a relatively stable and benign forest habitat preclude them from entering habitats that would call for coping with more extreme conditions of temperature and humidity? Vulnerability even within the zone of best adaptation may be seen in the fact that large tracts of forest are uninhabited, even though various lineages must have passed through them to achieve their present range.

Tree crickets (Oecanthinae). Tree crickets probably first colonized Kauai or Oahu (probably the latter), and within a span of 2.5 million years radiated into three genera (*Prognathogryllus*, *Leptogryllus*, and *Thaumatogryllus*), five subgenera, and 54 species, with the greatest diversification seen in the older islands (Figures 2A and B). Cladistics and biogeography suggest that nearly all speciation has taken place within islands.

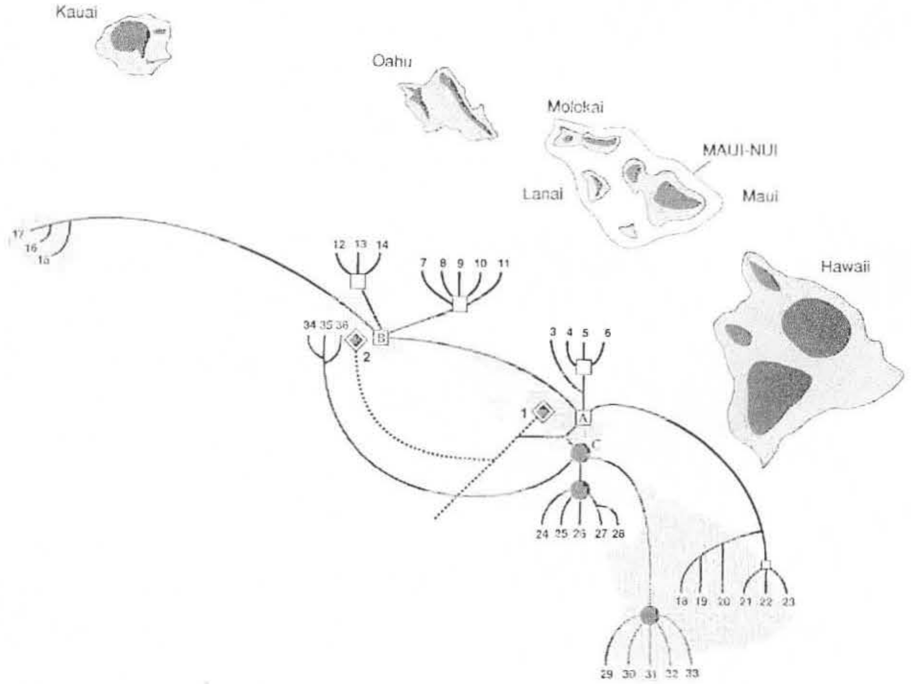

FIGURE 2. *Top*: Hawaiian archipelago showing the major highlands (black areas); Maui, Molokai, and Lanai were united into a single large island (Maui-Nui) during the Pleistocene. *Bottom*: Hypothetical phylogeny of *Prolaupala* (1,2) and *Laupala* (3-33).

This seems to agree with the speciation pattern see in some plant genera, such as *Cyrtandra* (with 129 species on Oahu alone), and in land snails, *Achatinella* (over 100 species on Oahu) (Carlquist 1980), but differs somewhat from that seen in Drosophilidae, in which a greater degree of between-island speciation may be common (Carson et al. 1970). Today 43% of the world's known tree cricket species are Hawaiian. Though this statistic can also be taken to reflect badly on the state of taxonomy elsewhere, the number of species is still impressive. Furthermore, diversity in form and ecology exceeds that of the remaining world's tree crickets; Hawaiian oecanthines have radiated into adaptive zones that elsewhere are occupied by the members of several other subfamilies. Some species have lost all traces of the sound-producing and -receiving apparatus, some have adapted to a life under bark, others hide in hollow twigs, some have become terrestrial, and still others are subterranean. From the standpoint of signaling the *Leptogryllus–Thaumatogryllus* group of genera are highly specialized members of the subfamily. The group has lost its sound-producing and -receiving structures completely and probably has adopted a largely olfactory mode of communication.

Sword-tail crickets (Trigonidiinae). Sword-tail crickets also appear to have originated on Oahu (or, less likely, on the Maui complex) between 1.5 and 2.5 million years ago and diversified into three genera (*Anaxipha*, *Prolaupala*, and *Laupala*), five subgenera, and more than 150 species. Although fewer adaptive zones were occupied as this group diversified (all species are at least partially arboreal, none has occupied caves, and no species has become mute), the speciation rate has been much higher. Unlike tree crickets, the diversity is higher in younger islands, with *Laupala* being much more diverse on the youngest island than on the oldest (Figure 2).

Ground crickets (Nemobiinae). *Caconemobius* is a genus of wingless and mute species derived from an oceanic group of crickets widespread through the Indian and Pacific Oceans and inhabiting seashores (coral and rocky outcrops and mangrove swamps) (Figure 1). In Hawaii it is represented by one species inhabiting the shores of all islands, and, probably derived from this shore species, an unknown number of inland species inhabiting lava crevices and lava tubes. Speciation in *Caconemobius* appears to be the result of the shore species repeatedly penetrating into island interiors along lava flows (either on the surface or below the surface, in crevices and perhaps in caves) and becoming isolated in different lava flows. The diversity of species seems to be inversely related to island age. The paucity of species on older islands may be due to habitat destruction—the disappearance of lava tubes and the extensive network of crevices, which become filled with erosional debris. A second genus, *Thetella*, is represented only by *T. tarnis*, a widely distributed species throughout the Pacific Ocean, from eastern Australia to Hawaii. The genus appears not to have speciated in Hawaii, perhaps due to its extraordinary vagility.

The introduced crickets. *Gryllus bimaculatus* (an Afro-Asian species) began its Hawaiian odyssey at the port in Lihue, Kauai. We know the year and even the month it must have entered. It was confined to the port area for about one year. Then, within months, it exploded to cover the entire island. It moved into all habitats except forest, on the wet as well as the dry side of the island, and now ranges from sea level to the high, often mist-covered central massif. Although it has since been reported in Oahu and Maui, it was not heard on these islands in August 1988. A second African species, *Acheta domesticus*, though it is widespread over the globe, is usually only locally distributed; in Hawaii it is known only from Honolulu and one small patch of desertlike habitat on the extreme west side of Kauai. *Teleogryllus oceanicus*, *Modicogryllus* sp., and *Trigonidomorpha sjostedti* are Asian species that are widespread in pastures, cane fields, and other disturbed habitats on all islands. Aside from *G. bimaculatus* we know little about when the last four species were introduced.

Distribution patterns. Taxonomic work shows some general patterns of distribution in numerous species, but reveals detailed patterns in only a few species (Otte and Rice 1989). Tree cricket distribution patterns vary considerably from island to island. On Kauai, *Prognathogryllus* is represented by several widespread species and a number of small peripheral isolates. On Oahu a greater proportion of the species are wide-ranging, resulting in considerable overlap among species. But the widest distributions of any *Prognathogryllus* species is still less than a large United States city, even though larger areas of suitable habitat appear to be available for colonization. The smallest distributions appear to be no larger than a few city blocks. By contrast, oecanthine species on the North American continent extend for many hundreds and even thousands of miles, and continental species introduced into Hawaii have colonized all of the Hawaiian islands. Distribution patterns of Hawaiian endemics suggest that some species originated within the overall range of the parental species and that virtually all speciation takes place within islands, much of it probably within volcanoes. Maui and Hawaii *Prognathogryllus* show how much wholly isolated cognate populations have differentiated. But what causes the species to break up into relatively small populations in an essentially continuous forest devoid of closely related (possibly competing) congeners?

THE CALLING SONG

In crickets it is possible to work directly with signals that we know the organisms themselves use to differentiate between their own and other species with whom they occur syntopically.[3] Readers may question the importance of song in the origin and maintenance of reproductive barriers among cricket species, particularly in cases in which song types are virtually indistinguishable morphologically. How do we know that song types correspond to what we normally think of as species? Differences in song within and between populations have, in all cases tested, been shown to be the result of genetic differences (Fulton 1933, 1937; Hörmann-Heck 1957; Bigelow 1960; Alexander 1957; Walker 1962). Sympatric (and syntopic) species virtually always have distinctive calling songs even when they are otherwise indistinguishable (Fulton 1952; Alexander 1962; Otte and Alexander 1983). No examples of within-population song varieties are known.

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[3] *Syntopic*: occupying the same microhabitat; *allotopic*: not occupying the same microhabitat even when sympatric (Rivas 1964).

These songs are intense, rhythmic sounds produced by males to attract sexually responsive females (Regen 1913; Walker 1957; Alexander 1960). Experiments show that females of some species can discriminate even between slight differences among syntopic species (Walker 1957). Since songs promote homogamy, song differences have long been thought to be important either in speciation or postspeciational adjustment of populations (Alexander 1957, 1960, 1962, 1968; Walker 1957, 1962, 1974; Bigelow 1960, 1964). All existing evidence points to the conclusion that the calling song is the most important (even if not the only) premating barrier in species that communicate acoustically. The fact that songs are under both polygenic and multichromosomal control is of interest given the theory that speciation may occur faster when the number of loci involved in reproductive isolation is larger than when it is small (Nei 1976; Nei et al. 1983).

Research on cricket signaling has focused more on the sender than on the receiver. To better understand the role of the calling song in speciation it is necessary to know more about the coordination between sender and receiver and how this evolves. Given that each permanent signal change must be accompanied by a change in receivers, how do the large differences that often characterize syntopic species evolve? Small changes in male signals can probably be more easily tracked by females and could in time accumulate to yield big differences. But are large changes always the result of a gradual accumulation of small changes, or can changes be saltational? Barton and Charlesworth (1984) note that reproductive isolation usually involves many genes and that this tends to exclude macromutations as a mode of speciation and that isolation is built up in a series of small steps. Field observations show that saltational variation does occur, although in cricket songs it is possible that a large phenotypic change could result from a minor genetic one. Whether large song changes in signaling can spread and become fixed depends on whether the receiving mechanism is functionally linked to it. We note three examples of striking, within-population variation:

1. On the slopes of Puu Kukui (West Maui) we heard a male of *Prolaupala kukui* switch back and forth between his normal rate of singing and a rate half the normal speed. Only one male was heard making the switch. In the eastern United States *Oecanthus fultoni* and *O. quadripunctatus* do this too, particularly when starting up singing in the early evening (Alexander, personal communication).

2. In *Anaxipha* sp. on the east slopes of Mt. Waialialae on Kauai, we heard a number of males switching back and forth between the normal song and a song with half the pulse rate. Although the species was distributed continuously for hundreds of meters, the peculiar song variation was found in a stretch of fern about 50 m long.
3. On Hualalai volcano above Kailua-Kona we heard three males, separated by 50 m or so, singing an abnormal song. The normal song was a trill, and these three males dropped pulses to produce an erratic song.

The examples show that the pulse-timing mechanisms may be altered to fire at half the normal speed. In the latter two cases, a mutation causing the change may have made its appearance at least in the previous generation. If the neuromuscular mechanism of sending and receiving are part of a single system, sons and daughters of the affected individual can simultaneously respond to the new pulse rates. A linkage allows sender and receiver to evolve as a unit and simplifies the process of evolutionary change in a communication system. Alexander (1962) asked: "Is it possible that in some or many cases the genetic difference that causes the song difference—perhaps even the particular difference in the structure of the central nervous system itself—is exactly the same as the difference that causes the response difference?" Huber (1962) showed that some of the components necessary for production of the song pattern may also reside in the female's nervous system. More recently it has been postulated that single neurons or networks of neurons could be involved in both the generation of temporally patterned signals and recognition of these patterns, i.e., the central pattern generators and neural filters/sensory-motor templates could be one and the same (Hoy 1978; Doherty and Hoy 1985).

There is still little direct evidence for a "hard-wired" sender–receiver coupling, and the results of crossing experiments are equivocal. Crosses between *Teleogryllus* species show that male F_1 hybrids have songs with spectral and temporal characteristics that are intermediate between those of the parents *and* F_1 females respond best to hybrid songs, preferring the songs of siblings over those of reciprocal hybrid crosses (Hoy and Paul 1973; Hoy 1974; Hoy et al. 1977). But since signal generation and recognition are both under polygenic and multichromosomal control (Bentley and Hoy 1972; Hoy 1974; Elsner 1974; Elsner and Popov 1978) it is to be expected that hybridization will yield intermediate neural pattern generators and sensory templates in hybrids. Therefore, sender and receiver mechanisms may be under separate genetic control. Even if sender and receiver mechanisms are genetically independent, signaling could become coordinated through coevolution (Helversen and Helversen 1975a, 1975b;

Elsner and Popov 1978; Doherty and Hoy 1985) and sender and receiver could in time become genetically linked.

Synchronizing behavior in *Laupala* (two species from Mt. Tantalus) suggests a close linkage between sound reception and sound generation. In these two species males close to one another often synchronize perfectly and instantaneously. In *O. fultoni* there is an entrainment period during which one male gradually comes to synchronize with a neighbor.

ORIGIN OF SONG DIFFERENCES

When do species recognition differences arise? What is their role in the acquisition of species status? Do they ever cause speciation? Muller (1942), Mayr (1963), and later Nei (1976) held that all or most signal differentiation among related species is probably due to incidental differences that evolve in a period of isolation, while Dobzhansky (1937, 1970), Lack (1947, 1971), and others thought that much (though not all) differentiation is due to coevolution taking place in sympatry. Alexander (1962) surmised that new modes of singing in crickets developed in connection with keeping interspecific confusion to a minimum. It is difficult to resolve this controversy, or to decide in any given case when signal differences arose, because conclusive evidence is extremely difficult to obtain.

Divergence during isolation (independent evolution)

How much differentiation takes place while populations are isolated? It is a certainty that the signals of isolates will diverge in time due to various factors acting individually or jointly: (a) selection pressures from the physical environment (Littlejohn 1988; Ryan and Brenowitz 1985), or (b) from the bioacoustic environment (Littlejohn 1988; Ryan and Brenowitz 1985); (c) effects of natural selection on other characters (Muller 1942; Mayr 1963); (d) effects of mutation and random sampling (Nei 1976; Nei et al. 1983); and (e) effects of social selection (West-Eberhard 1983). But what is the contribution of each, and can the differences that separate sympatric species be accounted for by these factors? To determine what kinds of song differences arise outside the influences of other species is difficult, for it requires locating species that are isolated not only from cognates,[4] but from all species with signaling systems similar enough to cause interference. Hawaii provides few such cases, and no instances in which a species is isolated from all other cricket species. The nearest we can come to complete isolation is to examine species that live only with members of unrelated genera whose songs are so different that they probably interfere only minimally.

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[4] *Cognates:* two daughter species, or a mother and daughter species sharing an exclusive common ancestry.

On both Maui and Hawaii a single lineage of *Prognathogryllus* has spread over each island and has formed isolated populations. The songs have diverged in some of the populations, in some cases only very slightly, in others sufficiently to suggest that species status has been reached. But the songs are not (with one exception) as different as among coexisting *Prognathogryllus*. The exception is the song of *P. waikemoi*, which is not only widely divergent, but is peculiar in having one of the most variable songs known in crickets. The possibility that the song evolved its high variability under conditions of relaxed selection is discussed in the following section.

Ecological release

Ecologists have considered the consequences of removing a species from competition with other species more than systematists have. Thus, Hutchinson (1958) speculated on how traits that act as intrinsic barriers to interbreeding might be affected by the number of related species: "When we have a great variety of allied sympatric species there must be an emphasis on very accurate mating barriers which is unnecessary where virtually no sympatric allies occur." Do organisms released from the competitive pressure of related species become less tightly adapted to a particular situation, and are elements of signals lost or do they become more variable? Lack (1971) notes cases in which fewer species on islands tend to have broader habitats and feeding stations than birds in richer mainland communities. On the basis of studies on island birds, Lack (1947) and P. Grant (1965, 1966) note that when species no long interact with related species, selection for species-identifying characteristics is relaxed and results in the loss of elaborate or distinctive morphology, evolution of much individual variation within species, and a return to simpler song types. Wilson and Bossert (1963) suggested that selection for species specificity of pheromones results in the synthesis of larger molecules, since the number of distinctive and unique forms that a molecule can take increases with its size. Available data on pheromones indicate that sex attractants, which demand high species specificity, are generally large molecules, whereas alarm and recruiting substances, which need not be highly specific, have lower molecular weights (Wilson 1971).

Among Hawaiian crickets the two species of *Prognathogryllus* that show the greatest amount of intrademic variability are isolated on Maui and Hawaii, respectively. *Prognathogryllus waikemoi* is so variable that after hearing the first three males of the species we believed that we had heard three different species. It is perhaps the most variable cricket song that has ever been recorded. In most *Prognathogryllus* (and crickets in general) temporal song rhythms are extremely constant and can easily characterize sympatric species. The song of this one species is as variable as the song of an entire genus. The only element of the song that remains constant is the pulse duration. Perhaps in this species individual pulses act as beacons of sound, while the interpulse intervals have become irrelevant.

Prognathogryllus mauka from the slopes of Hualalai and Mauna Loa on the Big Island is also highly variable; in this species, also, single pulses of sound may be produced.

It is difficult to argue from just two cases, but the complete absence of highly variable songs in multispecies communities supports the notion that song variability can be influenced by the presence of other species.

Character displacement and reinforcement (character coevolution)

To students of natural populations, divergence occurring between two groups in sympatry is inherently more interesting than divergence of geographically isolated groups. Brown and Wilson (1956) gave the name character displacement to the coevolutionary divergence occurring between populations living in the same area, which causes them to subdivide the resources of an environment on a smaller scale than they were subdivided previously. [Mayr (1963) used "character divergence" to refer to the same process, and V. Grant (1966, 1971) refers to it as the Wallace effect.] The term reinforcement has a similar meaning but was applied principally to coevolutionary enhancement of those signal differences that promote homogamy and at the same time discourage heterogamy. In spite of recent efforts to make the distinction between reproductive character displacement and reinforcement more explicit (Butlin 1985), the two concepts do not refer to two fundamentally different processes. Perhaps the terms are useful in defining when during speciation the coevolutionary adjustment occurs. If the groups involved are distinct species at the time they interact, their divergence may be called character displacement. If the groups are well on their way to becoming distinct species, the divergence should be called reinforcement.

Dobzhansky believed that character displacement commonly resulted from selection that enhanced sexual isolation—that the differences between coexisting species are "ad hoc contrivances" built by natural selection that guard against interbreeding. But the recent literature gives the impression that character displacement is rare, does not occur, or is unlikely (Paterson 1978, 1982a, 1982b, 1985; Butlin 1985; Carson 1986; West-Eberhardt 1983) and that differences are accidental by-products of divergence caused by other factors. Paterson states: "the isolating mechanism . . . which so much fuss has been made since 1935, comprise nothing more than an artificial, man-made class of 'effects.' They are, none of them, evolved adaptations to protect the 'integrity' of a species by preventing hybridization." My reading of Dobzhansky reveals no instance in which the character displacement (reinforcement) between cognates was not built upon a preexisting difference (evolved in allopatry)—a difference "visible" to, and improved by, selection.

Walker (1974) searched for examples of character displacement among United States acoustic insects (crickets and katydids) where two species in a zone of sympatry are more different than are allopatric parts of the same species. Not finding any convincing cases he asked: "Why should examples of character displacement be scarce in crickets and katydids?" He gives various possibilities:

1. Character displacement does not occur.
2. Character displacement occurs but is difficult to detect, perhaps because the process does not produce the pattern predicted by Brown and Wilson (1956). For example, a species might arise from a small peripheral population in which sympatric divergence could occur prior to the expansion of the new species into an allopatric range.
3. Character displacement occurs and produces the Brown and Wilson pattern but either not enough cases have been examined to properly assess how common it is, or the diagnostic pattern of character displacement is rapidly lost in the zone of sympatry as the trait rapidly spreads into the zone of allopatry.

Wallace (1968) and Hill et al. (1972) give an explanation of why few cases of character displacement have been discovered: a species could arise from another as a small border population; when this small population makes contact with the parent populations virtually all members of the daughter population interact directly with the parental population and are therefore under intense selection to acquire signal differences. The larger population is not under a similarly strong selection and may show no response to the presence of the smaller population. The expected result is that the small population will evolve in its entirety away from the larger population, while the larger popul[illegible] nchanged. Subsequently the daughter species expands to become largely allopatric.

Cricket taxonomists and biologists (beginning with Fulton 1933) have long noticed that the songs of coexisting (synchronic and syntopic) species are always widely spaced, whereas those of related species separated by geography or season are more similar and may even be identical (Alexander 1962). The theory that coexisting species probably adjust their songs one to another in a fashion that reduces signal interference and confusion is given credence by experiments that show that acoustical signals of one insect species may interfere with those of another (Walker 1957; Hill et al. 1972; Loftus-Hills et al. 1971; Otte 1979a). Paterson (1978) argues that such differences are accidental and are not the result of one species adjusting its song to that of another.

To examine the question of whether the differences among sympatric species are accidental or not, the dispersion (or spacing) of songs in the sound space among coexisting sets of species can be compared with a random dispersion. If spacing is found to be hyperdispersed (as taxonomists have usually assumed it is), then the dispersion may be due to direct interaction among species. Calculating distances between songs in the hyperspace is complicated when songs differ in a number of parameters (pulse rate, pulse length, chirp rate, chirp length, etc.). We have attempted the procedure in Hawaiian *Laupala*, whose simple songs differ only in pulse rate (i.e., they are very nearly arranged along a single axis of the sound space). We began by plotting the pulse rate of the 46 taxa at 68 localities where two or more species coexist (Figure 3). This gives a picture of spacing among the taxa making up each community. Song differences among these coexisting taxa were then assembled into a frequency histogram. We then took pulse rates of the same 46 taxa and reassembled them at random, producing the same number of communities and community sizes as before, but not allowing any taxon to be grouped with itself. Two such random assemblages and frequencies of differences are shown in Figure 3. The results indicate, first, that observed communities of species have a greater average separation than would be expected by chance alone, and second, that observed communities show relatively few instances in which closely similar song types coexist in one community. Such hyperdispersion is probably due directly to an interaction among the species.

However, these results do not tell how communities came to be spaced in this fashion. The pattern could be due to character displacement (a coevolutionary response) or it could be due to trial and error mixing, with only species sufficiently different in pulse rate in the first place being permitted to coexist in stable communities. In the first hypothesis, incompatible species become compatible through evolutionary changes; in the second similar (incompatible) species fail to mix, whereas dissimilar (compatible) species are permitted to coexist.

Can the results of coevolution and ecological mixing be distinguished? Coevolutionary effects would have to be discounted (1) if there were no greater differences in sympatry than in allopatry in taxa that have partially overlapping ranges, (2) if clines in two or more coexisting species either did not diverge or did not follow parallel tracks, or (3) if taxa living alone

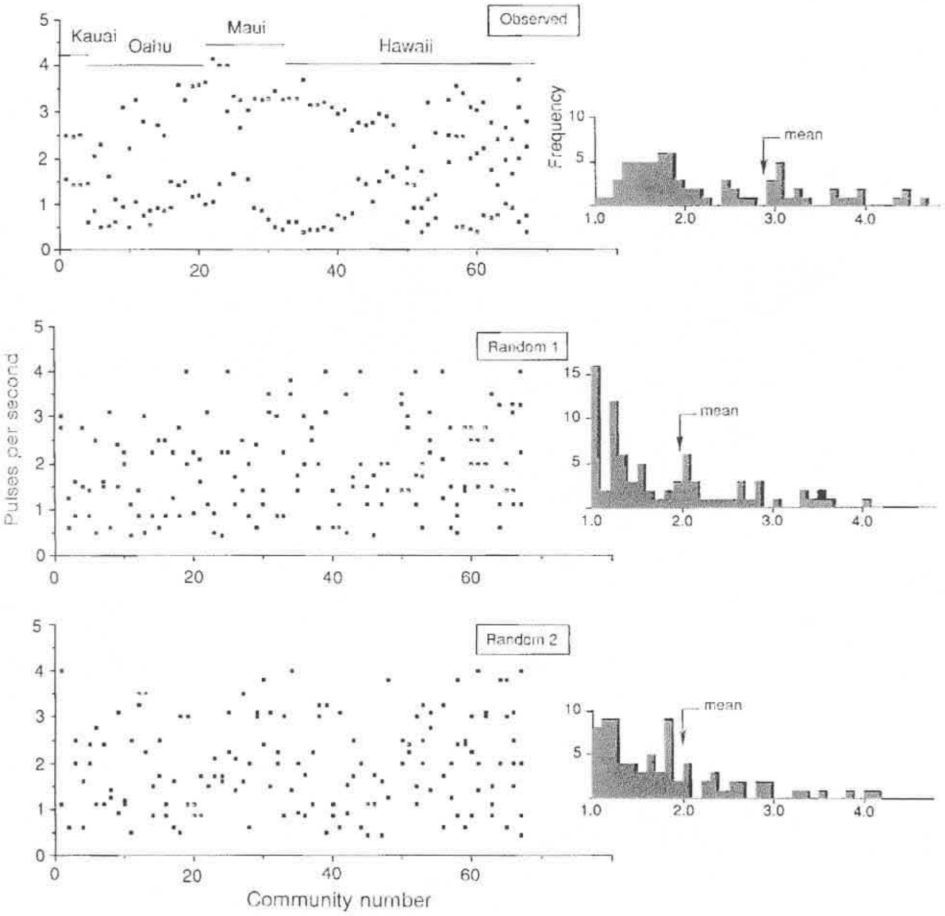


FIGURE 3. *Top*: Actual spacing of songs among syntopic *Laupala* species; each dot represents the mean pulse rate of each species at a locality. The histogram to the right plots the frequency of different degrees of spacing between neighboring song types in a community. Spacing on the (X axis) is calculated by dividing the pulse rate of a species by its next slowest neighbor (e.g., in the set of three species A = 4/second, B = 1.5/second, C = 1.4/second, spacing between A and B is 2.67, and that between B and C is 1.07). Spacing of 5.0 or greater is not shown. *Middle and bottom*: Random reassembly of song types from above into communities equal in size and in number to the above (but no song type is grouped with itself). Observed communities show a significantly lower than chance tendency for nearly identical song types to coexist.

showed the same or a lesser amount of phenotypic variation than those living in a multispecies community.

The distribution of *Laupala* species and the pattern of song within and between species is beginning to suggest that song differences are due to coevolutionary adjustments between interacting species.

Kaui. Song variation along a transect about 3 km in length (Kuilau Ridge Trail) (Figures 4 and 5) gives preliminary evidence of recent and perhaps incomplete speciation in *Laupala*. First results from a survey of songs along the transect come from the winter of 1977–78 (open histogram, Figure 4). The data indicate a single species at the upper end of the transect, and two well-differentiated species at the lower end. At two places along the transect the pulse rates of the common species were significantly slower (at zones D and E, Figure 4). Both slow-down zones were, at most, a few tens of meters wide. The presence of intermediate songs suggested that all songs were produced by one species. In my symposium presentation I suggested that the slowing down at these sites was perhaps due to the presence of an as yet undetected species. A survey conducted in the summer of 1988 revealed slower songs in precisely the same locales as in 1978 (areas 1 and 4, Figure 5). After correcting for effects of temperature (to 20°C), it became apparent that summer and winter songs were significantly different over much of the transect, especially near the upper end. The possible existence of two seasonally separated (allochronic) but syntopic species with slightly different song rates suggested an explanation for the slowing down of songs in certain places. A breakdown of the seasonal barrier in certain places could result in interbreeding and cause the slower, primarily winter species to adjust downwards relative to the slightly faster summer species. It was shown in Figure 3 that the degree of song difference displayed by winter and summer "species" does not exist among synchronic and syntopic *Laupala* species.

In December 1988 an additional 450+ males were tape recorded along the transect (Figures 4 and 5). These data confirm a seasonal difference in song, although the difference is less pronounced in areas 8 and 9 than elsewhere. Several differences between summer 1988 and winter 1988 are noteworthy (Figure 5).

(1) In area 1 the summer population of males has the appearance of a hybrid swarm (presumably between the summer and winter species). In area 4 song rates are clearly bimodal, suggesting the existence of two species, and the slow song type more or less replaced the faster type.

(2) The winter populations of males in area 1 are slower and less variable. In area 4 the absence of bimodality suggests that all songs are by a single species.

(3) There is an additional slow-down zone at area 6 that was not seen in the summer.

(4) At the lower end of the transect (area 10), two clearly defined synchronic and syntopic species are present both winter and summer in a thicket of hibiscus. But in the winter of 1988 the slow species was rare. These data also indicate a seasonality in the slow species in area 10.

A survey in December 1988 along the Powerline Road is shown in Figure 5. These songs have the same pulse rate as those across Keahua and Kawi streams. This survey was conducted to see if slower songs detected along this road in 1978 were present in 1988. Two areas with slower males were found at the same place as in 1978. The bimodal pattern suggests that there are two species here.

In summary, these preliminary data suggest the following hypothesis: there are three "species" along the Kuilau transect: a slow species at the lower end that is more common in the summer than in the winter; a summer species over the entire length of the transect (fastest song type); and a winter species (intermediate song type) completely syntopic with the summer species. Although summer and winter species are largely allochronic, separation of breeding seasons has broken down in several places where the winter form breeds all year round. Interbreeding with the summer species has caused considerable hybridization in area 1 and microgeographic parapatry in area 4. In both places the song of the rarer winter species has evolved to a slower rate (approaching the more normal separation between synchronic and syntopic *Laupala* species).

This interpretation hinges on the assumption that the differences in song are largely due to genetic differences, and the possibility that even tropical crickets can be highly seasonal. The long-term persistence of the slow down areas and the absence of geographic or ecological correlates of the slow-down areas suggests a genetic basis for the patterns.

On the matter of seasonality, we know of several *Laupala* populations on Kauai that are highly seasonal; in one of them males can be heard singing only in the summer. Since various species may be discontinuously distributed geographically in essentially continuous habitat, it seems reasonable to expect that temporal distribution may also be discontinuous and that seasonal separation of populations may also contribute to the extrinsic isolation of populations.

Regardless of what interpretation one adopts, the Kauai data give dramatic evidence of how sedentary and unchanging Hawaiian cricket populations are. In a flying species on a continent, small, locally adapted populations cannot become established since genetic novelties arising locally would be obliterated by the constant movement of individuals. It demonstrates the need to examine geographic variation in stable tropical areas on a very small scale.

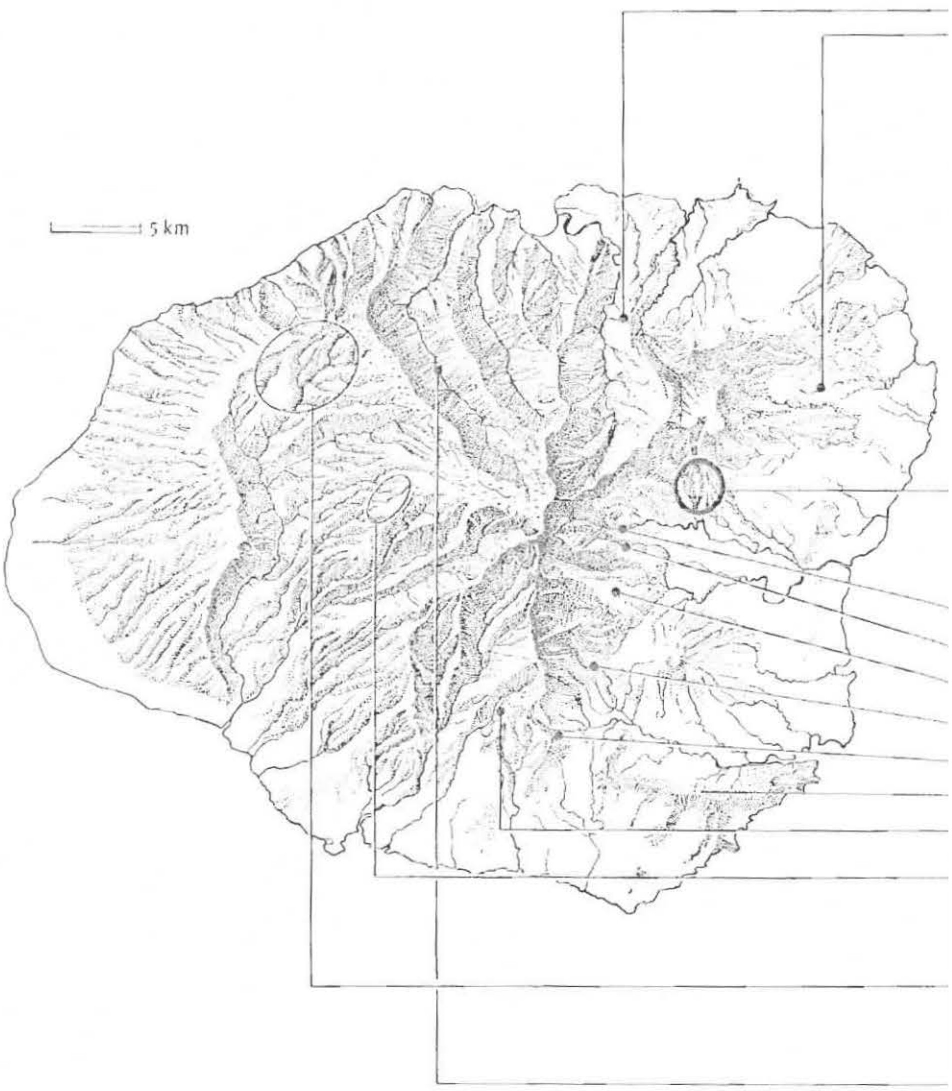
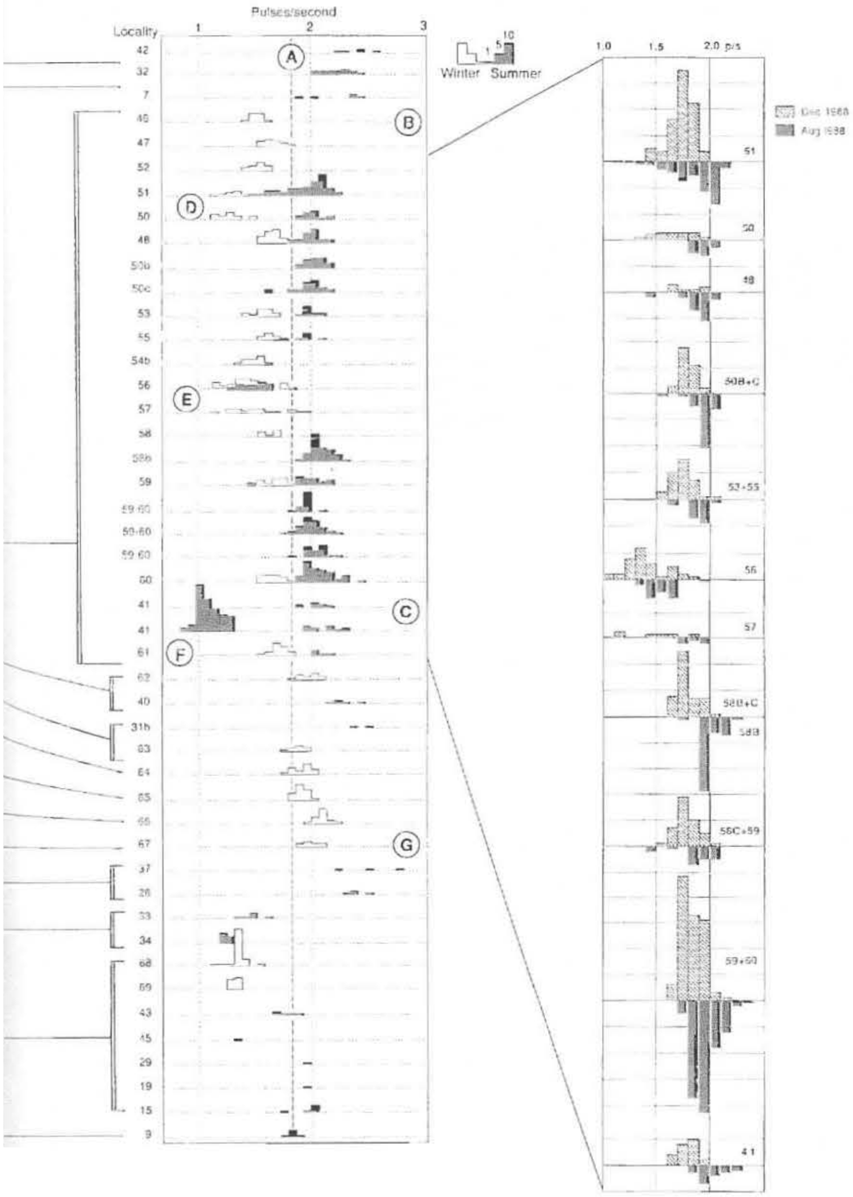


FIGURE 4. *Left*: map of Kauai. *Center*: Pulse rates among *Laupala* species corrected to 20°C. Open histograms: Winter data (Dec.–Jan. 1977–1978). Closed histograms: Summer data (Jun.–Aug.). In the transect B to C there are three "species": (1) a slow species at zone C; (2) a fast summer species (above dashed line); and (3) an intermediate primarily winter species (below dashed line). The last species has markedly slower songs at zones D and E, where it also breeds in the summer. At zone D (locality 51), intermediate songs suggest hybridization between summer



and winter species (better shown in Figure 5). At zone E the intermediate species replaces the faster species over a distance of some 60 m. The breakdown of allochrony between winter and summer species and consequent hybridization may have resulted in the evolution of slower songs in the winter species. *Far right:* Comparison of summer (Aug.) 1988 and winter (Dec.) 1988 data (corrected to 20°C) along the Kuilau transect confirms the summer–winter differences in song.

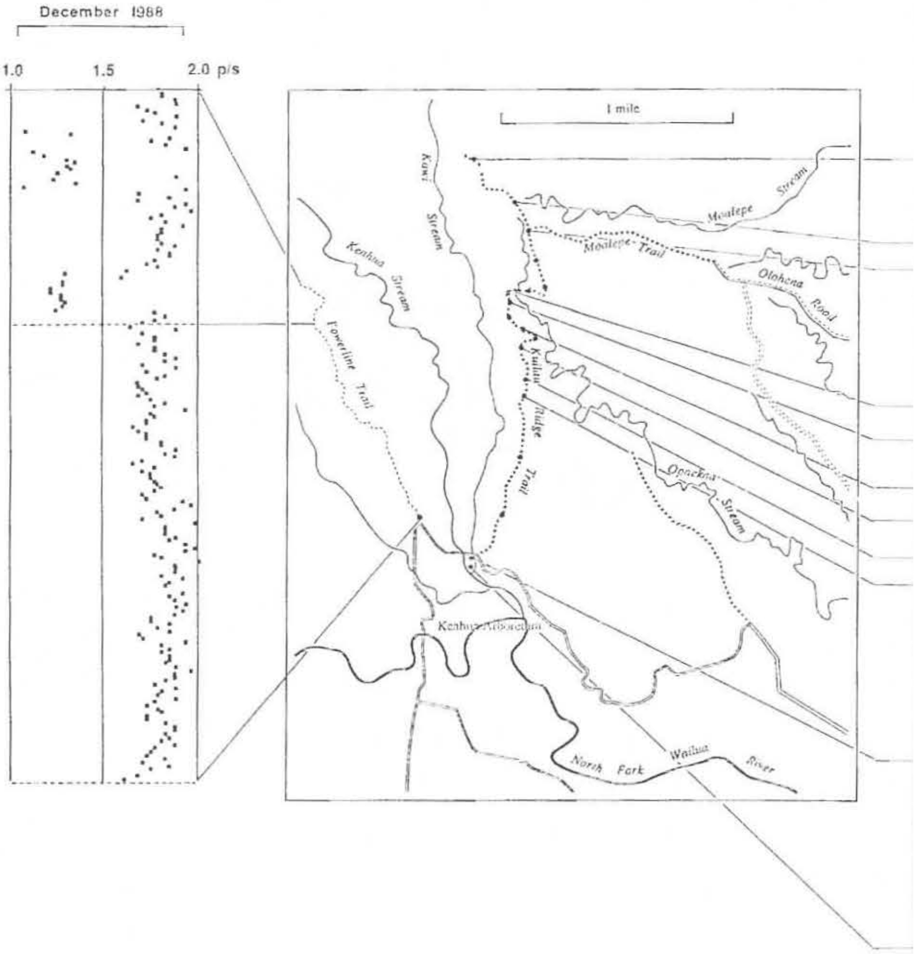
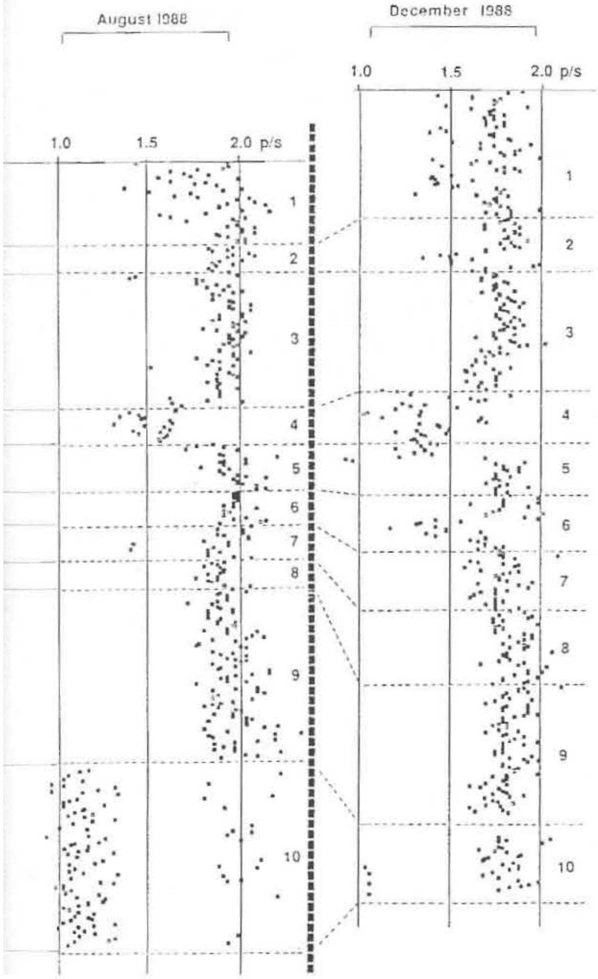
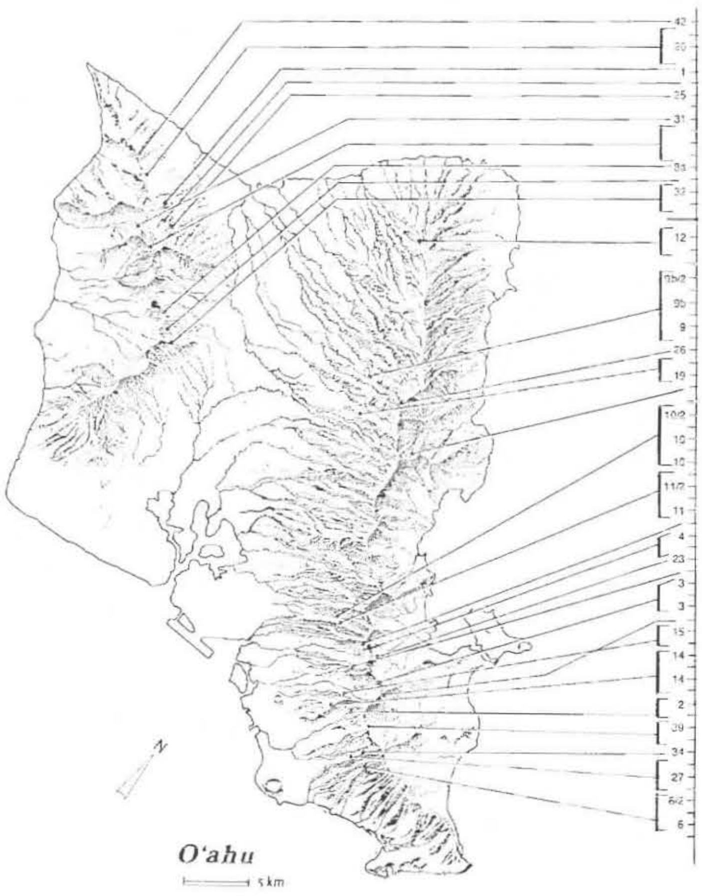


FIGURE 5. Comparison of pulse rates between summer (Aug.) 1988 and winter (Dec.) 1988 along the Kuilau Ridge and Powerline Trails. Each dot represents the pulse rate of a single male corrected to 20°C. These are arranged in the sequence in which they were recorded. The width of a recording area (1–10) is a function of the number of males recorded in that area. *Right hand scattergrams:* These diagrams show that the slow songs recorded in December coincide with those places where the winter species also breeds during the summer. It also suggests clinal variation in the winter species—for example from areas 3 to 4 and 7 to 6. There is also a greater tendency of the winter form to grade gradually into the slower song types; this may suggest a genetic continuity that is not as apparent between the common summer species and the slower song type. An exception is in area 1, where the summer species seems to grade into a hybrid population. *Far left scattergram:* Diagram shows a common species with pulse rates similar to the winter species along the Kuilau Ridge Trail and several small zones containing males



with slower songs. This pattern has also persisted for at least 10 years. The absence of intermediate songs suggests that speciation between faster and slower song types is complete. (See also Figure 4.)

Oahu. Transects on Oahu give a complicated picture in which putative species are geographically fractionated by ridges and valleys and in which the isolates show differentiation in song. Although we have tentatively grouped populations of singing males into "species" on the basis of their similarity, we do not know if isolated populations belong to the same species or not. Although detailed, meter-by-meter data on songs have not



been collected on Oahu, the overall patterns suggest a few intriguing possibilities.

1. At the southern end of the Koolau Range (at A in Figure 6) the song of the species *L. palolo* becomes faster where it overlaps with *L. spisa*.
2. Also in the same region, *L. tantalis* is more rapid in the region where it overlaps with *L. nui* than farther north. However, *L. nui* does not change its pulse rate in a similar fashion.
3. In region B there appear to be parallel clines between *L. nui*(?) and *L. palolo*(?).

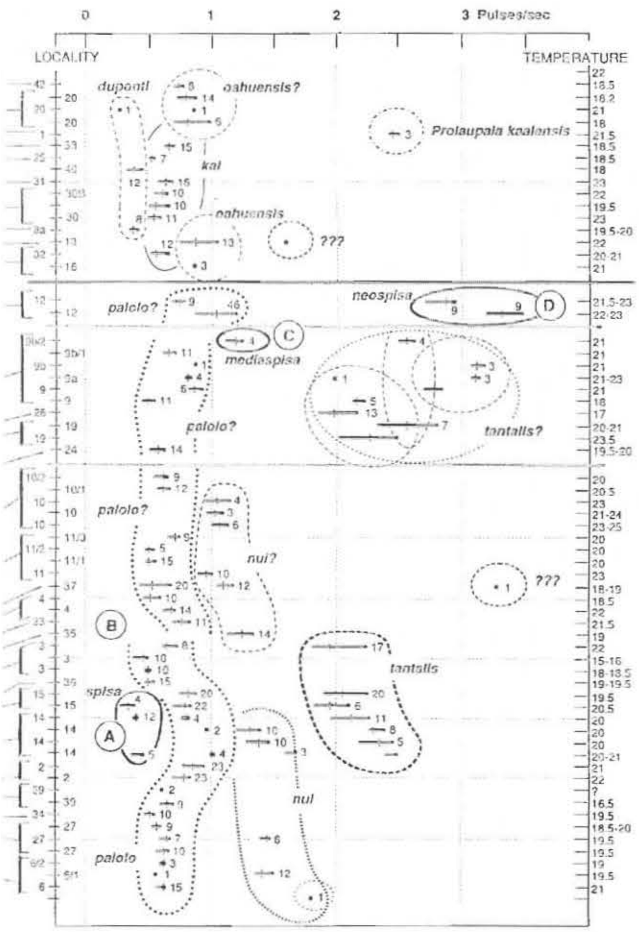


FIGURE 6. Song variation in *Laupala* species of Oahu (range, mean, and *N*). Song types are tentatively grouped into putative species on the basis of song similarity and, in some cases, morphology. Possible cases of character displacement are indicated by letters: In zone A the species *palolo* has a faster song where it is sympatric with the slower *spisa* than on either side where *spisa* does not occur. In the same region *tantalis* is faster where it is sympatric with the slower *nui*. Near zone B *palolo*(?) and *nui*(?) appear to have parallel clines. The Spisa group (*neospisa*, *mediaspisa*, and *spisa*—A, C, D) belong to a group which entered Oahu more recently than the Pacificum group (remaining species). If they are derived from a single introduction, then the group has fitted itself into three different parts of the acoustic environment.

4. The Spisa group, indicated by heavy lines at A, C, and D, is a group which probably came to Oahu from the Maui-Nui complex long after the Pacificum group (all other species) was established. The southern species (*spisa*) has the slowest song of any *Laupala* on the island, the northern species (*neospisa*) has the fastest song, and, in between, the third species (*mediaspisa*) has an intermediate song. If the three species in the group are indeed derived from a single ancestor, then the three lineages may have evolved in several different directions according to the mix of species each encountered. Ecologically, morphologically, and chromosomally these three species are indistinguishable. But the song differences are now so great that one wonders if the three song types would merge, even if no postmating barriers separated them. (But Littlejohn, 1988, argues against speciation operating in this fashion.)

Hawaii. Detailed transects on Big Island *Laupala* show the distribution of a number of putative species (Figure 7). One of the more interesting aspects of *Laupala* on Hawaii is the number of species along the windward slopes. At the north end there are two species. The number of species then increases in the central section (slopes of Mauna Kea) and decreases to one species on Kilauea and Mauna Loa. Coinciding with the greater number of species is a spreading out of the pulse rate such that the fastest and slowest species are to be found in the region of greatest diversity. A number of clines are also to be seen in this region. We can focus on some of the more interesting parts (Figure 7).

1. In sp. 1 there is a steady north to south cline in region A (localities 29X to 75) after which the pulse rate levels out. This may be due to the presence of sp. 5 in this part of the forest.
2. The songs of sp. 3 and sp. 4 are most similar to one another in region B, but that of sp. 4 appears to be displaced where it is syntopic with sp. 3. Farther north it becomes sympatric with sp. 4 and becomes faster still. At regions C and D there is evidence from songs that some hybridization occurs (Figure 8).
3. It is possible, and perhaps likely, that spp. 1-4 each represent several species. Only detailed, meter-by-meter surveys of song changes can give one a better information of numbers of species and interfaces between species. Also, it is likely that species separated by season will be discovered.

The overall impressions gained from Big Island data are, first, that the spreading out of the pulse rates is greatest where species are most numerous. Second, the divergence in signals seems to be greater between coexisting populations than between allopatric populations. Third, the example of two species with parallel clines suggests a coevolutionary response in two species.

Summary

Patterns of song variation in *Laupala* lead to these tentative conclusions:

1. Song evolution seems to be molded by the bioacoustic environment and particularly by the signals of more closely related species; character displacement is probably common in Hawaii and elsewhere, even if the principal clue—clinal character displacement in a zone of overlap—is rarely seen; if character displacement is common, then reinforcement must also be common (though less frequent than character displacement) for there must be situations in which speciation is incomplete. The phenomenon may seem to be rare only because it is difficult to see. Character displacement and reinforcement—similarly difficult to see—may initiate many of the key recognition differences we see among species. To see examples it is necessary to be in precisely the right circumstance, or arrange for it to occur.
2. The high variability seen in *Prognathogryllus* species that are isolated from all congeners tends to support the notion that the presence of other species causes songs of a species to fall within fairly narrow limits or to be fairly invariable; it is a difficult proposition to prove because there are species in Hawaii and elsewhere that have relatively invariable songs; it is noteworthy, however, that such variable songs are unknown in species that live in multispecies communities.
3. Some transects in *Laupala* show marked divergence occurring over short distances (tens to hundreds of meters). It seems likely, given the close proximity and absence of noticeable distribution gaps, that a genetic continuity exists.
4. Mayr favored an allopatric origin of behavioral reproductive barriers and yet saw an important role for ecological character displacement in speciation: "Those individuals of two overlapping species would be most favored by selection that have the least need for the resources jointly utilized by both species." He does not say why premating barriers would not be affected similarly. In *Laupala* species, the songs diverge while ecology remains unchanged.
5. Lande's (1980) notion that "In a population which is geographically isolated from the main range of a species, reproductive isolation can evolve only incidentally as a by-product of genetic divergence occurring for other reasons," is not justified insofar as the "isolated" deme may be influenced by related species other than cognates; therefore reproductive isolation evolves under the influences of the same kinds of pressures.

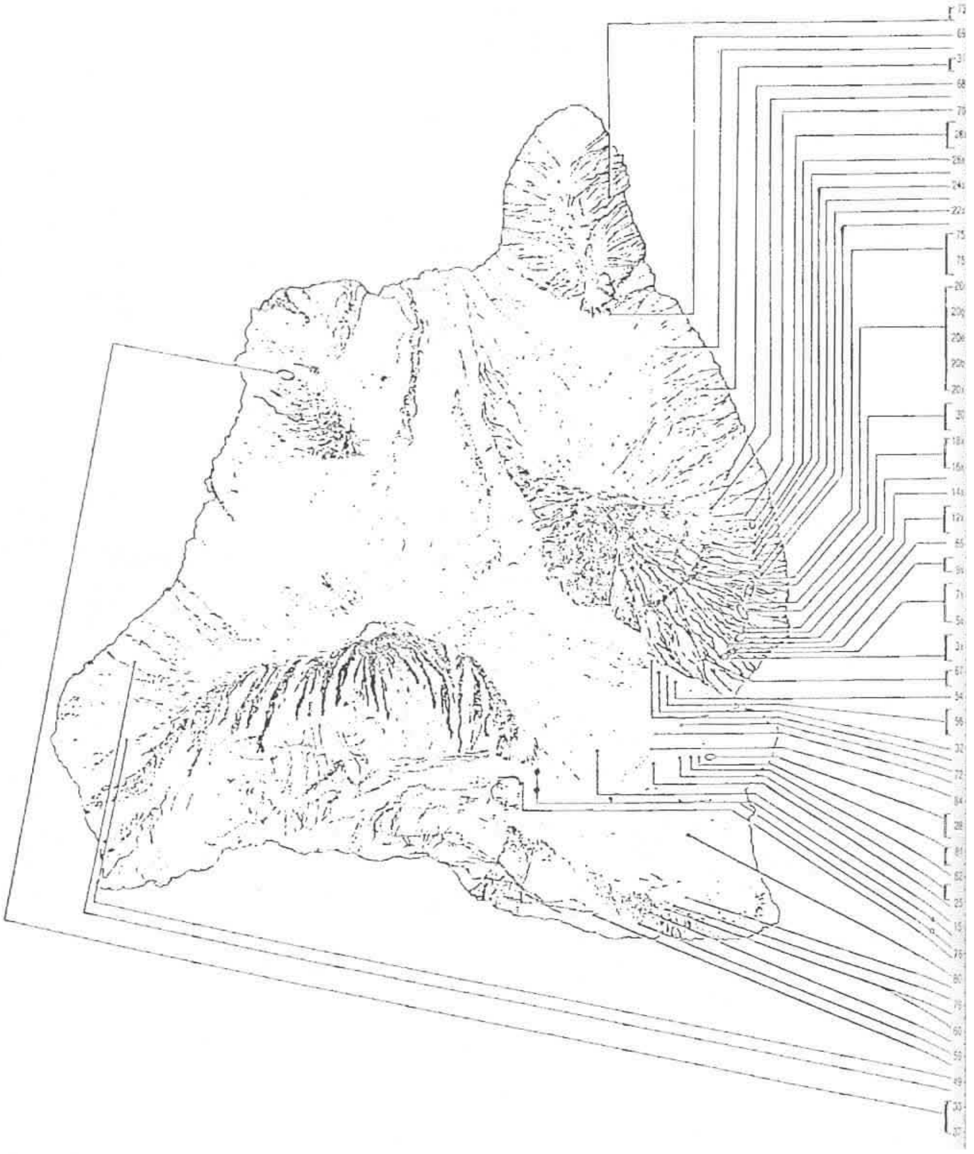
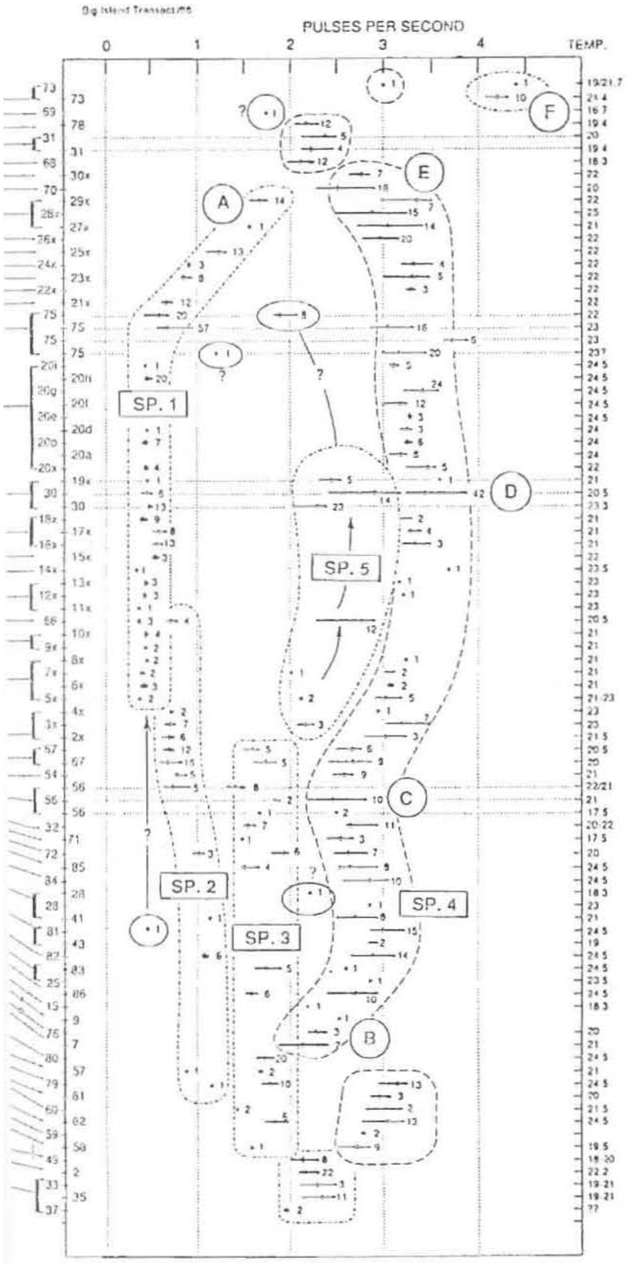


FIGURE 7. Song variation in *Laupala* species of Hawaii (range, mean, and N). Songs are tentatively grouped into putative species on the basis of song similarity, geographic continuity, and morphology. Sp. 1 shows a steady cline in pulse rate in zone A, perhaps due to the presence of a species with an intermediate song. The songs of spp. 3 and 4 are more similar to one another where they are allotopic than



where they are syntopic. The song of sp. 4 is faster where it is sympatric with sp. 5 than at either side where sp. 5 does not occur. Some hybridization between spp. 4 and 5 appears to be occurring at D (see Figure 8).

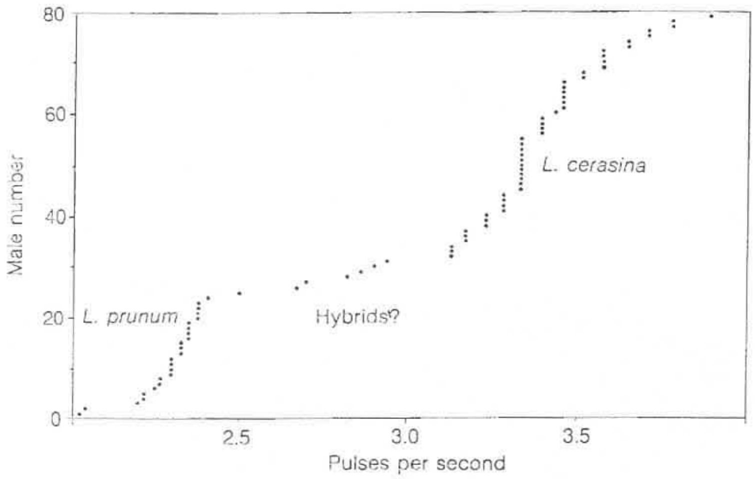


FIGURE 8. Plot of slowest to fastest males at Akaka Falls (D of Figure 7) of sp. 5 (*prunum*) and sp. 4 (*cerasina*). Intermediate songs may be of hybrids.

6. Paterson's (1978, 1982a, 1985) arguments that signal differences are due to pleiotropic effects are weakened by the fact that species that are highly divergent in songs cannot be distinguished on any other grounds—morphological, ecological, or genetic. Also, his theory does not explain why sympatric species, including siblings, are, as a rule, unambiguously distinct, whereas allopatric, geographically separate populations are not. The possibility that noncognates play an important role in molding the signals of a species is not discussed.
7. Carson's (1986) assertion that hybrid disturbances "do not serve as selective forces that elicit and strengthen premating incompatibilities, as is often assumed" probably derives from his theory that speciation is initiated and completed by founders in Hawaiian *Drosophila* (discussed under the section "Breeding Structure"). Earlier Carson and Kaneshiro (1976) had noted the importance of elaborate species-specific courtship behavior as barriers to interbreeding (see "Social Selection and Sexual Selection"). To Dobzhansky (1972b) the correlation in Hawaiian *Drosophila* between diversity in courtship and mating pattern and species diversity meant that the former was not an accidental byproduct of genetic divergence. Evidence for character displacement (and reinforcement) in this genus comes from the field (Kaneshiro 1976: "Pronounced sexual isolation is observed between the sympatric species, *heteroneura* and *sylvestris*, and further documents the concept that premating isolating mechanisms evolve as *ad hoc* products of selec-

tion between sympatric species") and has been demonstrated in laboratory studies (Knight et al. 1956; Kessler 1966).

ECOLOGICAL ISOLATION

Coexisting species usually differ in their ecological requirements if they are very closely related. This separation, though not usually believed to lead to the formation of new species, is often thought to be essential if species are to coexist syntopically. Lack (1971) in particular stressed the importance of acquiring ecological differences as a contrivance to permit coexistence: "Two species of animals can coexist in the same area only if they differ in ecology. Such ecological isolation, brought about through competitive exclusion, is of basic importance in the origin of new species, adaptive radiation, species diversity, and the composition of faunas." The notion that ecological differentiation must take place mostly during allopatry is also noted by Littlejohn (1988), who supposes that "adequate ecological differentiation in cognate populations during a disjunct allopatric phase is an essential preadaptation for coexistence" and Dobzhansky (1972b) who noted that "ecological isolation, genetically conditioned preference for different habitats, is in a sense intermediate between geographic and reproductive isolation."

Our data on Hawaiian crickets are not yet exact enough to make firm statements concerning the point at which ecological divergence takes place, relative to song divergence, but they are suggestive (Otte and Rice 1989). For the most part, the species believed to be particularly closely related often have what appear to us to be virtually identical ecologies. Carson and Stalker (1969), Heed (1971), and Carson and Kaneshiro (1976) note similar trends in *Drosophila* where subspeciation does not appear to be based primarily on ecological differences of neighboring regions, and most related species have closely similar ecologies.

In *Laupala* comingling species often show no seasonal, daily, microhabitat, or foraging differences, although slight morphological differences are often evident. Consequently we are inclined to the view that ecological differences often arise after species have come into contact. The songs and life cycles of the three *Laupala* species on Kauai (Figures 4 and 5) are noteworthy, however, in showing pronounced seasonal differences. Diurnal differences between species having nearly identical songs are seen in pairs of *Anaxipha*. Along Wahiawa Stream on Kauai two species have nearly identical songs: one species sings mainly in the daytime from under the bark of *Metrosideros* trees; the other species sings at dusk and at night in underbrush and ferns beneath the same trees. At Kaulalewelewe (West Maui) one species sings in the ferns and leaf litter close to the ground in the daytime, and is replaced by another species that sings from ferns and low tree foliage at night. The members of each pair are not cognates of each other. In both instances we cannot know without further geographic and ecological evidence whether the ecological differences coevolved in sympatry or whether preexisting differences allowed the similar song types to coexist.

How might ecological separation between cognates be achieved? We suggest the following sequence: Nearly identical species with confusingly similar signals are prone to interact and to suffer from communication interference; those insufficiently differentiated cannot coexist and displace one another to form parapatric distributions (sometimes in a mosaic pattern corresponding to their initial numbers or to differential competitiveness in a mosaic habitat). From this parapatric situation they could begin to adjust to one another ecologically, behaviorally, or both, at the zone of contact and slowly penetrate one another's ranges. Species with preexisting differences (visible to selection) can coexist at the start, but may continue to diverge if differences facilitate coexistence.

SOCIAL SELECTION AND SEXUAL SELECTION

The role of sexual selection in Hawaiian speciation has been discussed in several recent papers (Ringo 1977; Kaneshiro 1983; Carson 1986). Perhaps it was the amazing array of morphological and behavioral traits in Hawaiian insects that led *Drosophila* biologists to suspect that sexual selection has played an important role in speciation. West-Eberhard (1983) argues that social behavior may have played an important role in speciation in many groups: "Many species-specific signals heretofore attributed to selection for species recognition . . . are probably instead products of social selection."

Ringo (1977) speculated that directional intrasexual selection in Hawaiian *Drosophila* during isolation causes the sender–receiver system to evolve away from the ancestral condition through a Fisherian runaway process. Postmating barriers then evolve as pleiotropic effects of this evolution. The problem of how the runaway process is initiated, particularly given the usual tendency of signaling systems to be highly uniform within populations, is not discussed. Also, the obvious association of the great divergence of displays in Hawaiian *Drosophila* with high diversity of species (more than 60 in the Waikemoi area of Maui) suggests an interspecific cause and effect relationship. Carson and Kaneshiro (1976) noted that *Drosophila* "exhibit elaborate, species-specific courtship behavior which evolved as a major isolating mechanism among related species." Later, however, Carson (1986) suggests that the difference arose mainly during geographical isolation of the cognates.

I will attempt to evaluate the role of intraspecific relations in molding cricket acoustical signals. Because it is not always clear to me what form of sexual selection is referred to, or when sexual selection should be invoked in accounting for evolution of cricket song, I shall begin with a clarification of what I believe is meant by this term.

The sexual selection concept has been the source of much confusion (O'Donald 1980) perhaps because "the evolution of differential adaptation of the sexes is an exceedingly complex subject" whose analysis "demands integration of information and theory from several biological disciplines" (Selander 1972). Confusion existed in Darwin's own mind (although O'Donald claims otherwise). His contemporary, Wallace (1889:296) thought it was "really a form of natural selection" whose "results are as clearly deductible as those of any of the other modes in which selection acts." Huxley (1938) remarked: "None of Darwin's theories has been so heavily attacked as that of sexual selection" and he suggested that the concept be replaced by two terms: "epigamic selection" in which one sex exerts an influence on the other, and "intrasexual selection," which involves competition between members of the same sex. Mayr (1972) also reviewed this topic and concluded that many traits whose origin was ascribed to sexual selection were better explained through natural selection, whereas Selander (1972) maintained that "Strictly speaking all characters directly affecting reproduction should be attributed to sexual selection, including those that facilitate copulation and fertilization and those involved in parental care." Ehrman (1972) defined sexual selection as "all mechanisms which cause deviations from panmixia." O'Donald (1980) may not have clarified the matter by insisting that "sexual selection must be distinguished from assortative mating" and speaking of a separate "theory of assortative mating." Furthermore, in his discussion of the evolution of mating preferences he comes close to maintaining that natural and sexual selection are different phenomena: "Natural selection must now be incorporated in the model of the evolution of mating preferences in order to analyze the sequence of events in Fisher's general theory of sexual selection."

Sexual selection in its pure form was defined by Ghiselin (1974) as selection in which "the females receive no benefit from mating with one male rather than another." This definition derives from Fisher's (1930) notion that there may be situations in which it is advantageous to display in a certain way only because the opposite sex prefers individuals with such displays—even though there is no measurable benefit to preferring one trait over its alternative. This is a special mode of selection that comes about after a population is brought into a particular circumstance through ordinary natural selection. It was this mode of selection that caused Fisher to suggest his now famous (but unproven) runaway selection process.

The impression is given, therefore, that there are two kinds of selection in nature: natural and sexual. I believe this is a false dichotomy, and that the use of the sexual selection label may actually obscure the precise nature of selection pressures in any given situation. Natural selection should, of course, be distinguished from artificial selection and cultural selection (learned behavior that could affect heritable traits). Subsumed under natural selection are as many components as there are selective agents or as the imagination will allow. Temperature, light, predators, parasites, food, related species, and conspecifics are all components of selection. Each component is further divisible; conspecifics include offspring, members of the same sex, and members of the opposite sex, and each of these is further divisible by age category, by relationship, by mode of interaction, etc. Furthermore, the various components interact with one another in multifarious ways. They can act, simultaneously or sequentially, to produce or maintain adaptiveness. Since different forces tend to push populations toward different optima they often have opposing effects. The result is that all organisms have compromised phenotypes. "Runaway" sexual selection is not unique in this—predatory pressures also force organisms into adaptations that reduce their adaptedness with respect to other traits (e.g., feeding, mating, camouflage).

The term "social selection" (West-Eberhard 1983) was coined to collect the various intraspecific interactive effects under one umbrella, including those components usually referred to as sexual selection, and including culturally transmitted traits. The concept is very useful as long as its noncultural parts are not thought of as anything more than components of natural selection. A difficulty with the concept of social selection as well as with sexual selection, as given by West-Eberhard, is its emphasis on competition: "*sexual selection* refers to the subset of social competition in which the resource at stake is mates. And *social selection* is differential reproductive success due to differential success in social competition, whatever the resource at stake." All symbiotic relations are a potential source of selection.

Searcy and Andersson (1986) have correctly emphasized that selection pressures from within a species (or deme) and those exerted by other species on a signal system are not mutually exclusive. It had been proposed, for example, that speciation may initiate the evolution of sexually selected traits (Trivers 1972; Emlen 1974) in this way: When two populations that have recently speciated begin to interact, selection is expected to favor females that can distinguish between the two kinds of males. According to one such scheme, females are least likely to make mistakes *by preferring the appropriate extreme* of an available sample. The process is initiated by ordinary natural selection, with the ultimate selection pressure for change coming from the presence of another species; since female preference leads to increased female fitness, there is no need to invoke sexual selection. However, the stage is now set for the operation of sexual selection in its pure form, for a point is reached at which females no longer make mistakes, but because the mode of choosing males (preferring the most extreme males) persists, male signals continue to evolve along the same track. In the absence of opposing selection pressures, such an "overshoot" could cause a much greater divergence between species than what is necessary for females to discriminate.

The role of social selection (noncultural variety) in signal divergence in crickets, as I see it, is depicted in Figure 9. Prior to a change in the species mix, the signaling system is at equilibrium with only small mutual adjustments occurring between the sexes. The influence of one sex on the other is mostly of a stabilizing kind, with major changes in one sex being inhibited when there is a failure in communication. (Rapid changes in the species mix such that a communicative system does not have enough time to adjust to a given mix would have the same effect.) A relatively permanent change in the species mix, however, can suddenly change the signaling environment. Species with closely similar signals must suddenly cope

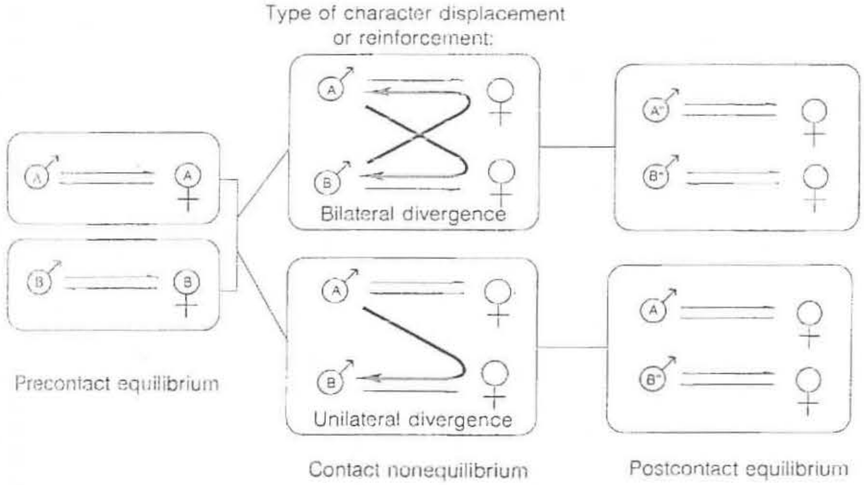


FIGURE 9. *Precontact equilibrium*: Under stable conditions male-female signal systems are likely to be at equilibrium and generally stabilizing. *Contact nonequilibrium*: As two previously separated species begin to mix (interact) the initial influence is the presence of males of another species; females, in adjusting to the new acoustic environment, then bring about a change in the signal code of their own species. Both species may adjust to one another (top center) or, if species A is common and species B rare, B may evolve much more than A. *Postcontact equilibrium*: In the upper case A has evolved into A', B has evolved into B'. In the lower case A remained unchanged while B has evolved into B'.

with signal noise, signal interference, and the risk of fruitless reproductive interactions. As species begin to mix ecologically, the initial influence is simply the presence of males of another species. Now, if the females adjust to the new acoustic environment by changing the rules of mate selection, they will also bring about a change in the signal code of their own species. Thus, we see that social selection can be seen to be a consequence of the disturbed equilibrium brought on by the introduction of extraneous males.

Whether one or both species change (bilateral divergence versus unilateral divergence) depends on the relative numbers of the two species, with females of the minority species being under greater pressure to change than females of the majority. Sawyer and Hartl's (1981) model predicts that natural selection for mating aversion is more likely to evolve first in the population that is rarer in the sympatric zone.

Our data on crickets do not indicate that sexual selection plays an important part in signal *divergence* between species. This mode of selection is not expected to have the same outcome as does signal coevolution. For example, it predicts that diverging taxa (populations, demes, or neighborhoods) will evolve largely independently of other taxa; it does not predict hyperdispersion of signals in the signal space; nor does it predict that coexisting populations of two species will differ more than allopatric populations or that clines will be parallel or divergent, or, in the absence of other species, that the signaling will become more variable.

Finally, the social/sexual selection theory of divergence cannot readily be distinguished from adaptive peak shifts predicted by Sewell Wright's (1932) shifting balance process. Under that process, small, semiisolated populations can diverge from one another and settle on different adaptive peaks, neither one necessarily superior to the other. Intraspecific sexual selection predicts the same outcome from a different mechanism.

The feasibility of a runaway process in crickets (in accounting for large differences between males) depends on how females perceive and respond to males. There are several alternatives: First, a female could choose males on the basis of an absolute standard (neural template of Hoy et al. 1977) regardless of its distribution in the population (*absolute preference model* of Lande 1982). Under this model we would expect female preferences to evolve to a point at which females can no longer perceive those males whose signals overlap with another species. Concomitantly, male signals will shift in accordance with the new female preferences, and cause sending–receiving systems to evolve nonoverlapping distributions, but then stop.

Second, a female could choose a male after comparing him to others or in relation to the population mean (*relative preference model*). Under this model the reception of signals is less constrained, and, provided it is consistent in direction with respect to the mean, could cause signals to diverge well beyond the point of overlap. Whether the choice is absolute or relative depends in part on what kind of signal is transmitted. Signal intensity would be particularly subject to change through a relative preference and evolve continuously in one direction. But female crickets choose males principally on the basis of pulse repetition rate. The mechanism is probably one in which the females perceive (or are wired to respond to) only a narrow range of pulse rates. The alternative to having a narrow perception/response window is having a wide window within which the female must "decide" among the items she perceives. The latter capability would probably require a more complicated neural apparatus that is able to compute a variety of rates and then make a decision among them. Is it possible for female crickets to pay attention to more than one song at a time or be able to remember one song as she listens to another? Such feats would seem to be required under the relative preference model.

If females do not choose by comparison, there would seem to be less opportunity for Fisherian runaway selection and songs will not diverge much beyond what is necessary for recognition. However, I noted previously the occurrence of species whose signals have diverged *well beyond* the point of overlap (these can also be seen in Figures 6 and 7). The possible explanations for such divergence are (1) the signals diverged by the runaway process after an initial episode of ordinary selection; (2) signaling and receiving could be structurally and physiologically coupled, allowing large changes in males to be tracked by females; large changes would be favored relative to small changes if they made a greater improvement in communication; (3) if signals always interfere with one another in some degree, no matter how different they are, then selection for divergence may continue indefinitely toward some asymptote; (4) the differences were acquired in a selective regime that no longer exists.

OTHER FACTORS INFLUENCING SPECIATION

Distance from source areas

The most conspicuous feature of Hawaii's biota is not its overall diversity, which is low by tropical forest standards, but the fact that some of its genera are enormously rich in species. This genus-poor and species-rich balance can be traced to one overriding factor—its great distance from, and tenuous connection with, its source areas. The distance causes few colonists to contribute to the eventual makeup of a saturated community of species. In islands closer to continents a larger number of colonists contribute to the final biota and result in the lower ratio. The high ratio in Hawaii is the single most important factor that contributes to the impression of a high speciation rate. Consequently it may be premature to conclude that speciation in the Hawaiian biota is faster than tropical forests elsewhere.

Island barriers

The usual kinds of impediments to gene flow have probably operated to fragment crickets. But since most speciation seems to occur within islands, we are naturally interested in just what kinds of within-island barriers are involved. Typically, Hawaiian islands pass through a number of developmental stages that affect the kind, number, and duration of geographic and ecological barriers and therefore must affect speciation in an important way. But the effect of topography on differentiating Hawaiian biotas has never been explored in detail. Here I will mention several stages in this evolution, and suggest how spatial heterogeneity changes and how habitat configuration might affect the opportunities for differentiation.

Lava fields, kipukas, and succession. In the early island-building stages relatively gentle eruptions produce extensive lava beds underlaid by lava tubes (tube-like caves varying in diameter from centimeters to tens of meters). Even before ecological succession produces forest on the surface, these lava fields can be colonized by *Caconemobius*. Within decades of an eruption, forest begins to cover the lava on windward slopes, thereby altering *Caconemobius* habitat and becoming habitable to a variety of forest-inhabiting species (such as *Laupala* and *Anaxipha*). Meanwhile, the lava tubes also become optimal for *Caconemobius* habitation as roots from the overlying forest penetrate into them to provide nourishment (Howarth 1973; Gurney and Rentz 1978). These lava caves descend the slopes in parallel and are largely isolated from one another. Cavernicolous populations of *Caconemobius* may be established mainly through founder events, and, being highly linear, may be particularly susceptible to isolation by distance.

During this phase forests may be continuous over large sections and be intersected here and there by a set of parallel lava beds originating as separate streams descending from an erupting rift zone. These flows incinerate the forest and leave behind isolated forest patches of various sizes and shapes. These are, therefore, classic vicariance events that may (1) divide a large forest patch into two, (2) divide a section of forest into a series of narrow, parallel forest strips, and (3) flow around higher spots, leaving behind various habitat islands (kipukas) that can vary in area from many hectares to a few square meters. Although the forest is maximally subdivided during this stage, subdivision of the biota lasts only for as long as it takes succession to restore the forest (decades on windward slopes, tens of decades or more on drier leeward slopes) and there may not be sufficient time for speciation. Phenotypically, crickets isolated in kipukas cannot be seen to be differentiating. Indeed, an important role for kipukas in Hawaiian speciation has not yet been demonstrated.

Forest and gulch. Following cessation of the eruptive phases, volcanoes pass through a long period (tens to hundreds of thousands of years) during which their lower slopes are covered by a continuous cloak of rain forest. Impediments to lateral movement (along the slopes) would seem to be minimal, but increase gradually as numerous parallel gulches develop. Our data show that although crickets readily cross gulches in the early stages, speciation is already much in evidence during this phase (see Character Displacement and Reinforcement); this must mean either that there are imperceptible extrinsic barriers, or that speciation takes place in their absence.

Plateau and valley. As gulches deepen and become united through erosion, the land comes to consist of plateaus and deep V-shaped valleys. Habitats then consist of forest and bog on the plateaus, valley bottom forest, and whatever vegetation can grow on the steep valley walls. The transitions between habitats constitute major ecological barriers. The habitat in the valley floor is very narrow, causing cricket populations to have a linear configuration.

Ridge and valley. Erosion eventually removes many of the plateaus and produces a set of narrow, parallel ridges. Upland forest and valley bottom forest now both force crickets to assume a strongly linear configuration. Later, as the ridges are worn down, forest trees return to the slopes and the linearity of distributions is diminished.

Ridge and alluvial plain. In the final stages as ridges erode away, alluvium collects on the valley floor and produces flat plains along the rivers. Thus, ridge top species continue to be linearly distributed whereas valley bottom species assume a less linear configuration again.

These various geological and phytogeographic features may act in combination, particularly with climatic stability, to facilitate speciation. The role of forests in restricting movement of insects that have become flightless is probably important.

Climatic stability

The stability and persistence of Hawaiian habitats permit small populations to survive for long periods; small effective population sizes, in combination with the linear distributions produced by the ridge and valley system in turn could influence the fine-tuning of isolated and semiisolated populations to local conditions. Extreme humidity and temperature sensitivity in crickets (in comparison to continental crickets) (Otte and Rice 1989) are probably a result of an unchanging environment that no longer selects for animals that can cope with climatic fluctuations, but instead selects for animals that fit into very particular ecological situations. Migration in such species must be selected against because the animals are either unlikely to survive conditions during or after migration, or to be competitive in new species mixes. The higher tolerance of continental crickets can also be seen in the much greater ecological amplitude of the introduced crickets compared to the Hawaiian endemic crickets. Because of the evolution of low mobility, the Hawaiian habitats become coarse-grained, with successive generations all inhabiting the parental patch type. Such constancy facilitates the development of precise relationships among syntopic species, on a scale not possible in areas in which migration is constantly mixing the species. An even spacing of songs is most likely to be seen in such a situation.

Have the continental crickets introduced to Hawaii begun to respond to the stable climate? In the case of *Teleogryllus oceanicus* we suspect so. Although long-winged individuals are produced, no migration by night-flying individuals (of the sort that is common in Australia) has ever been detected by entomologists who pay attention to such things. Whether the most recent immigrant, *Gryllus bimaculatus* (discussed in Background), now loses its tremendous migratory tendencies should be watched carefully over a period of decades. We suspect that countless individuals must already have been lost at sea as this species made its way down the archipelago. Similar net losses every generation are bound to select against migration and constitute the first stage in selecting for a more speciation-prone organism.

Reduced tendency to migrate may already have evolved in the grasshopper *Schistocerca nitens*, a highly migratory species in the continental United States and Central America. This species, introduced within the past 50 years, is found in large numbers at south point on Hawaii Island where it inhabits grassland and shrubs immediately adjacent to sea cliffs. At this locality a constant wind blows over the land and out to sea. Unlike the normal condition in *Schistocerca*, flushed grasshoppers here fly for short distances and only into the wind. I observed two individuals near the sea cliff that were being blown out over the sea; both attempted to return to land for at least 10 minutes before they were blown away to sea.

Breeding structure

Evolution within lineages and splitting of lineages are probably strongly influenced by the breeding structure of a species (Wright 1940, 1978; Barton and Charlesworth 1984). The breeding structure is defined by several population parameters that can influence the rate at which evolution occurs and the probability that a species will become fractionated. It is influenced by effective population size, proximity of neighboring demes, migration rates among demes, and the configuration of groups of demes. The breeding structure in Hawaiian crickets must be profoundly influenced by various geological events that affect habitat shape (see Island Barriers), as well as the abundance and strength of extrinsic barriers. It also is influenced by the mobility of the animals, which is probably a result of habitat stability (see Climatic Stability).

Founder effects

Remote isolates are given great evolutionary importance by proponents of speciation through founder effects (Mayr 1963; Carson 1971; Templeton 1981) but far less importance by proponents of the shifting balance process (Wright 1940, 1978; Barton and Charlesworth 1984; Barton, this volume) or by supporters of vicariance speciation.

The mode of divergence leading to speciation in Hawaiian *Drosophila* has been the subject of much thought and modeling. What proportion of speciation events is initiated by founder events as compared to vicariance events? From the fact that cognate species of *Drosophila* often live on different islands, Carson proposed a mode of speciation in which single foundresses play the most important role in speciation in this group. But vicariance events would seem to be a viable alternative in some Hawaiian groups, such as *Achatinella* (snails), *Cyrtandra* (plants), and crickets. Vicariance events in *Drosophila* cannot be ruled out; phylogenetic data based on chromosome banding patterns show that cognates or near-cognates frequently live on one island (Carson et al. 1970; Carson and Kaneshiro 1976).

The existence of sharp clines (differentiation with distance) in crickets raises the possibility that disruptive selection is an additional mechanism leading to speciation. The operation of such selection in the Hawaiian fauna remains unexplored, for it requires extremely detailed examination of geographic variation in phenotypic and genotypic traits.

There can be little doubt that founders have been important in speciation, but controversy surrounds the question: How important are the properties of the founders themselves in causing speciation? Carson (1971, 1973, 1982) proposed that a new species is founded by a single gravid female of an aberrant genotype that manages to reach another island. Such an unusual female is the product of a population flush arising from particularly favorable conditions that allow all sorts of unusual genotypes to survive and propagate, which, under normal conditions, would not survive. The theory assumes that the important genotypic change has already occurred in the founder on the island of origin. Templeton (1980b) supports Carson's theory, stating that the founder effect may be important in Hawaiian *Drosophila*, but does not believe that the process is important in *Drosophila* generally.

Wright (1978) criticized Carson's "flush-founder" theory on the grounds that it requires a double miracle: first, the essential change leading to speciation is an extremely improbable event, and second, this recombinant must then be isolated on a new island by another event of extremely low probability. As an alternative, Wright (1978) proposed the following:

> Under a more typical operation of the shifting balance process, the founder may be a fairly ordinary representative of its species that gives rise to a new species on reaching another island by the accumulation of new interaction systems under the exceptionally favorable conditions for the process there, especially while its local populations are sparse. Under this view, speciation by isolation in different valleys on the same island is not ruled out . . . The trial and error process among numerous small local populations by which control continually shifts from old selective peaks in sets of gene frequencies to new ones, each clinched by local mass selection and spread through the species by interdeme selection, does not require the double miracle of origin of a specific difference by recombination, and isolation of the same individual by being carried to another island. This is not to deny that if the founder is a wide deviant it may give a good start toward speciation in producing a population that comes at once under control of a new selective peak.

Time effects

Older areas are more likely to have more species than younger ones, other things being equal. But in Hawaii other things are not equal: in crickets and other groups, diversity seems to depend greatly on the order of colonization (on time since colonization). The effect of time is confounded by the fact that habitat heterogeneity also changes as islands age. Also, some components of heterogeneity (i.e., subdivision of forest by lava) do not decrease as islands age. *Caconemobius* and *Laupala* diversity is inversely related to island age and geological heterogeneity (being highest in the youngest islands); in the former the greater diversity is probably the result of the disappearance of the lava habitats that the members of this genus inhabit; in the latter case the diversity is probably related to where the genus originated in the islands.

SUMMARY

1. Hawaii's enormous species-to-genus ratio is a consequence of its great distance from its source areas.
2. The endemic cricket fauna appears to be derived from four original colonizing species, belonging to three subfamilies.
3. Cladistic and distribution patterns suggest that most speciation takes place within islands.
4. Hyperdispersion of songs among syntopic *Laupala* species indicate competitive interactions among species having similar songs.
5. *Laupala* systematics indicates that speciation can occur in continuous forest, before the development of major barriers (ridges and valleys).
6. Patterns of geographic variation in song among sets of species (greater divergence in signals between coexisting populations than between allopatric populations) suggest the existence of signal coevolution among syntopic species.
7. Hyperdispersion, character displacement, and increased variability of songs in isolated species are not predicted by the social or sexual selection models that emphasize within-species selective effects.
8. The high variability seen in *Prognathogryllus* species isolated from all congeners (along with the absence of variable songs in species that live in multispecies communities) supports the notion that the presence of other species causes songs of a species to fall within fairly narrow limits.
9. The influence of one species on another probably extends well beyond the point at which they no longer interbreed; a selective influence of one species on another may cease only when the songs no longer interfere with one another; therefore theories of reproductive character displacement should take into account a somewhat broader network of interactive effects and not just relations between cognates.
10. In the signal coevolution model the influence of one sex on the other is probably mostly of a stabilizing kind, with major changes in one sex being inhibited when there is a reduction in communication. But a change in the species mix introduces a fundamental new element in the signaling environment: the presence of males of another species. Changes in female responses to the new environment may cause reverberations through an entire intraspecific signal system.

11. Character displacement is probably extremely common in Hawaii and elsewhere, but would be difficult to detect if its principal clue—character displacement in a zone of overlap—is short lived. If character displacement is common, then reinforcement must also be common, for there must be many instances of interaction between taxa that have not completed speciation.
12. The possibility that signal differences in Hawaiian crickets are due to pleiotropic effects is weakened somewhat by the fact that species that are highly divergent in songs are barely distinguishable or not distinguishable on other grounds—morphological, ecological, or chromosomal.
13. Closely related Hawaiian species tend to have nearly identical ecologies. Ecological differentiation among syntopic species may often come long after behavioral reproductive barriers have been perfected.
14. The stability and persistence of Hawaiian habitats probably permit local populations to survive for long periods and adapt to local conditions, and selects against emigration. Forests may have a large effect in restricting the movement of flightless crickets, breaking a species up into many local demes and thus affecting the population breeding structure.
15. Eruptive and erosive forces in Hawaii promote the development of linear habitats (lava islands, lava tube, ridges, valleys) that could increase the opportunities for isolation by distance.
16. Because of low mobility, habitats tend to be course grained, such that successive generations all inhabit the parental patch type. Such constancy may facilitate development of precise relationships among syntopic species, on a scale not possible in areas in which migration is constantly mixing species.
17. The existence of sharp clines (differentiation with distance) in *Laupala* raises the possibility of disruptive selection as an additional speciation mechanism.

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